CHAPTER 9. SPAR AND THE PHYSIOLOGICAL PROCESS LEVEL MODEL

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Early crop simulation research (McKinion et al., 1975) demonstrated the futility of the "standard plant" concept, i.e. attempts to extrapolate with models based on data from field plantings. This problem was addressed by the development of the soil-plant-atmosphere-research (SPAR) system (Phene, et al., 1978). A SPAR unit, diagrammed in Figure 1, is capable of the independent manipulation of individual physiological processes. The early research also demonstrated the necessity of a two-dimensional model of the rhizosphere to account for the effects of dislocations in water and nutrient supplies to the plant roots in row crops. That problem was addressed in the construction of the root-rhizosphere model, RHIZOS (Lambert, et al., 1976). Thus, the SPAR system was designed for the express purpose of process level simulation modeling.

The SPAR concept constituted a major advance beyond the conventional phytotron in several ways. The system was vastly less expensive and therefore much more easily accessible to the whole-plant modeler. Each aerial chamber receives natural solar radiation, and light attenuation by the structure is much less than in the phytotron. Plants are grown in a row crop configuration, and the units are designed with vertical shades simulating within and between row light competition. The SPAR crop is grown in a soil medium and the front wall of the soil bin was made of wire reinforced glass to permit visual observation and measurements of the root system. Later SPARs have soil temperature control. Air and soil temperature, atmospheric CO_2, and irrigation are all controlled by the computer system which provides a real time log of crop environmental variables and rates of photosynthesis, respiration and transpiration.

Thus, SPAR provides the capability to characterize the effects of various environmental factors, singly and in combination, on the various physiological process rates and organ abortion. For example, photosynthesis and photosynthate supply/demand ratios can be manipulated simply by varying the concentration of CO_2 in the SPAR atmosphere.

SPAR also provides an efficient way to evaluate model performance over its (designed) ecological range prior to field validation, i.e. a range of temperatures or soil water conditions can be provided in one experiment and rates of photosynthesis, transpiration, respiration, leaf development, tiller production, the timing of heading and the abortion of tillers or spikelets can be measured. All these data can then be compared to these events and rates predicted by the crop model. Examples of SPAR data constituting the data base in WINTER-WHEAT are presented below.

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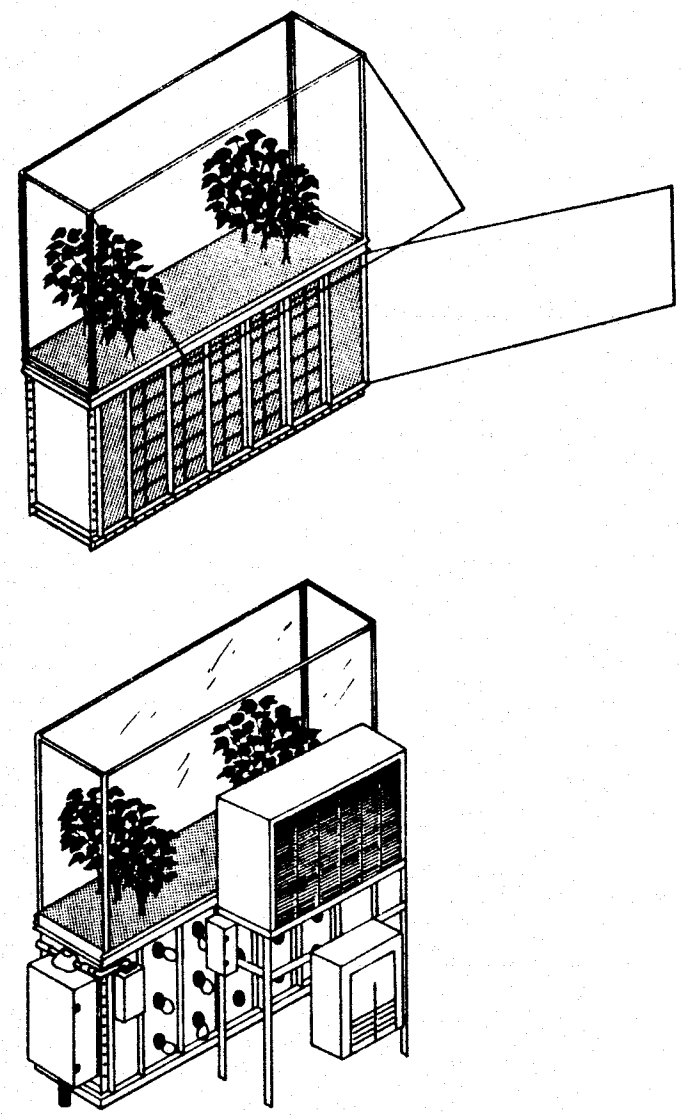

Figure 1. Front and rear views of a Soil Plant Atmosphere Research (SPAR) unit showing plexiglass top and soil bin with glass panels at front and instrument ports at back. The size of the air conditioner is exaggerated in this diagram.

PHOTOSYNTHESIS AND RESPIRATION

In 1976 at Florence, SC, three SPAR units containing Scout wheat were operated with three temperature regimes. The intermediate temperature treatment (SPAR B) represented a typical seasonal temperature pattern in the northern Great Plains. Low temperature (SPAR A) and high temperature (SPAR C) treatments were applied in the other two units; these treatments were 5°C higher and lower than the intermediate treatment (Table 1). This resulted in three different rates of plant growth, development and senescence.

An infrared gas analyzer was used to monitor and control atmospheric CO_2 in the SPARs. Each chamber was sampled once per minute. Carbon dioxide removed by photosynthesis was replaced by timed injections. The CO_2 control set-point was 320 $\mu l\ l^{-1}$. Vertical screens were maintained outside the units to simulate within and between row light competition. At several stages of development, canopy apparent photosynthesis and respiration were made via this closed system technique.

The Norfolk sandy-loam soil in the SPAR units was maintained with abundant mineral nutrients and water throughout the growing season. The soil bins were insulated but not temperature controlled. Throughout the experiment the plants appeared to be typical of healthy, vigorous crops grown in the Great Plains.

The respiration data presented in Figure 2 are typical of those obtained in this and numerous other (unpublished) SPAR experiments with wheat. Two techniques are commonly used in these measurements. In the first, the chamber is quickly darkened after a period of photosynthesis (Figure 2a). In the second, the chamber is kept dark for a period of 18 hours prior to and during the respiration measurements (Figure 2b). Rate of in-chamber atmospheric CO_2 increase is measured after 25 to

Table 1. SPAR Unit Temperature Control Program for 1976.

Day of Year	Average SPAR Air Temperature °C SPAR UNIT		
	A	B	C
6-12	2.7	5.3	9.8
13-19	4.6	7.2	10.1
20-26	4.9	7.1	12.8
27-33	4.6	9.7	12.8
34-40	7.2	10.2	15.6
41-47	7.2	12.8	18.3
48-54	7.2	12.8	18.3
55-61	10.0	15.5	21.1
62-68	10.0	15.6	23.9
69-75	10.1	18.0	23.5
76-82	12.6	18.0	23.6
83-89	13.1	18.3	25.8
90-96	15.9	21.2	29.3
97-103	16.0	23.9	29.4
104-110	18.2	23.9	29.3
111-117	18.2	23.8	28.8
118-124	17.9	24.1	29.3
125-131	19.0	23.8	28.7
132-138	18.0	23.0	27.4*
139-145	16.8	23.8	
146-152	17.2	23.9	
153-159	17.1	23.8	

*Terminated after day 137

30 minutes' of plant adjustment to a new temperature level.

Unlike the results with cotton (Baker et al., 1972), in wheat we have found no difference in rate of canopy respiration whether preceded by a period of rapid photosynthesis or not. The crop grown at high temperatures (SPAR C) was well into senescence when these measurements were made. Therefore, those data points were deleted in the analysis of the data. The relationships between respiration rate and temperature were not significantly different after periods of rapid photosynthesis, or after a long exposure to darkness. Therefore the light and dark respiration data were pooled and fitted to a single curve for use in the simulation model.

The technique for "light" respiration measurement may be criticized because it is, in fact, a respiration measurement made in the dark and used to represent respiration in the light (Chollet and Ogren, 1975). Although we believe any quantitative error will be relatively small, this estimate of the respiratory loss in the light will probably be on the high side. Canvin (1970) presents evidence that dark respiration may be reduced in the presence of light.

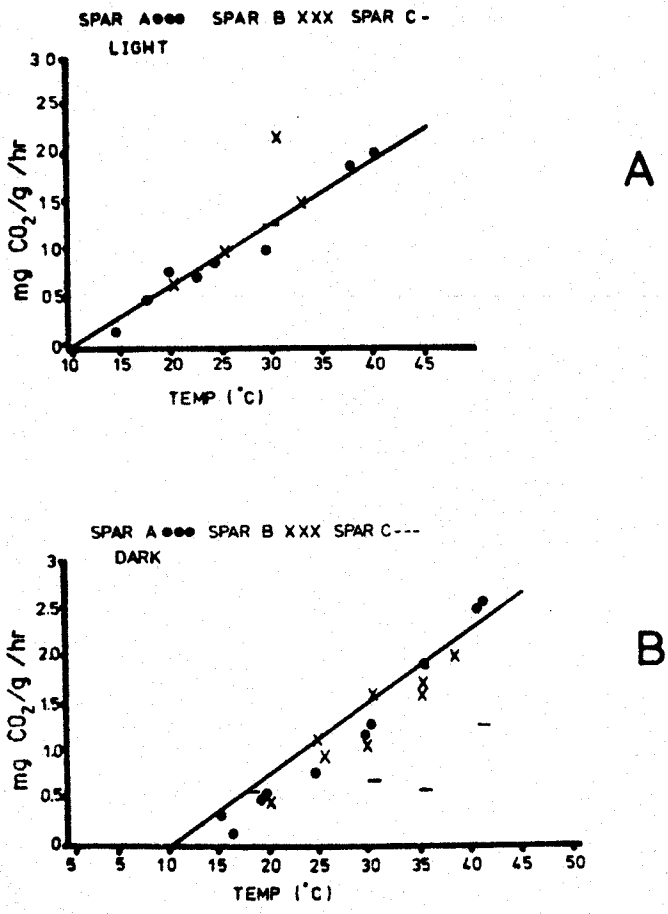

Figure 2. Canopy respiration rates (in mg. CO_2/gram dry plant weight/hour) vs. air temperature immediately after exposure to bright light (A) and after exposure to long periods of darkness (B).

There appeared to be no change in canopy photosynthetic efficiency during the season until the beginning of senescence. The effect of canopy senescence can be seen in the light response curves in Figure 3. There was no significant senescence in SPAR A noticeable through days 126, 127, and 128.

Appropriate dark respiration values from the above measurements were added

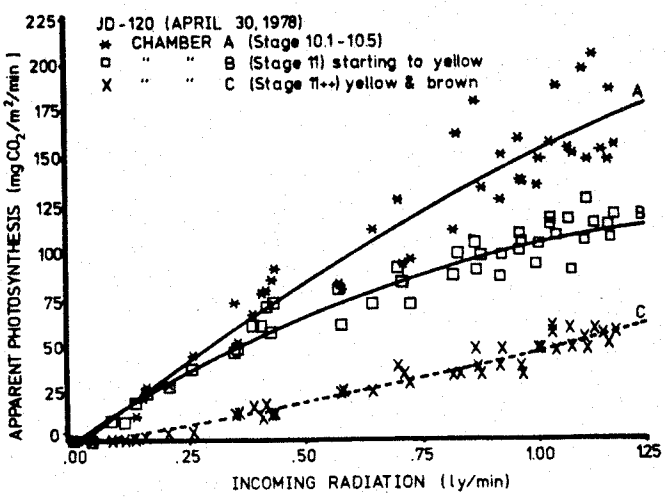

Figure 3. Apparent canopy photosynthesis vs. solar radiation flux density in three SPAR crops differing in maturity.

to these (15-minute) apparent photosynthesis values, and, the data were pooled to obtain a composite canopy light response curve (quadratic) with 258 15-minute data points. An R^2 value of 0.89 was obtained. This curve was used, with 15-minute average incoming solar radiation data throughout the daylight periods in 36 representative days over the season to produce the daily total data presented in Figure 4. The data range from completely clear days to completely and heavily overcast days. In the first draft of the PNET subroutine of the WINTER WHEAT model, leaf area was used to calculate canopy light interception and this equation was used to calculate daily photosynthate production from daily total solar radiation. Subsequent SPAR experiments in which soil nitrogen and water supplies were varied have provided empirical reduction factors both for direct effects on photosynthesis and respiration and the indirect effects due to stress induced changes in senescence rates.

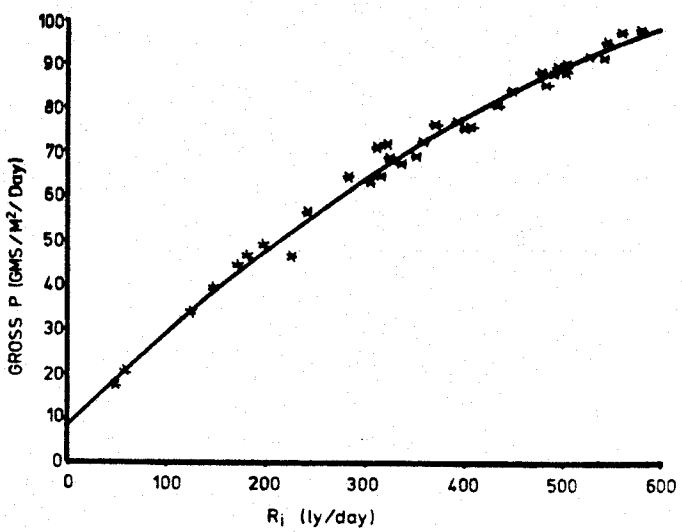

Figure 4. Daily total canopy photosynthesis vs. daily total solar radiation.

GROWTH

As noted elsewhere (Baker, et al., 1985), modeling strategy dictates that "genetic potential" rates of plant growth and development are characterized in the initial SPAR experiments. After the "genetic potential" growth and development rates are defined, other SPAR experiments characterize the effects of various stresses in reducing plant growth and development. Stress is defined as any factor which limits organ expansion, and this may include a carbohydrate source: sink imbalance. In SPAR experiments, sink strength is manipulated by varying plant turgor, temperature, and mineral nutrients. Carbohydrate supplies are manipulated by varying atmospheric CO_2 concentration and photosynthesis.

SPAR data files on the rates of wheat organ growth and plant development under nonstress conditions are now extensive, although few have been published. Typical data for leaf area and head growth (from Eissa, et al., 1983) are presented in Figures 5 and 6. Four SPAR units containing winter wheat (cv. Scout) were maintained at 600 $\mu l\ l^{-1}$ atmospheric CO_2, and supplied with abundant soil water and mineral nutrients. Temperature programs similar to those illustrated in Table 1 were maintained. The final air temperatures are included on the figures to indicate the temperature treatments. The time courses of head dry matter and leaf area accumulation are graphed against heat sums computed from a 0°C base.

Figure 5 shows that prior to 500 heat units leaf area growth was exponential. At that time LAI's were about 4, there 18 tillers per plant, and tillering was continuing. Due to the large numbers of tillers and leaves, the succeeding linear growth period probably represents a photosynthate limiting situation with growth rate of the total leaf canopy proportional to photosynthate supply. Weather source limited, due to the large number of growing tillers and leaves, or not, the rate depicted here should represent a useful maximum.

At the end of the vegetative growth period the plants were thinned to 3 to 5 tillers/plant. Average head dry weights are graphed against calendar date in Figure 6. The initial slopes are similar regardless of temperature, and the slopes during the grand period of grain growth are similar. However, temperature had a major effect on grain yield through its effect on the length of the grain filling period. Thus, the primary effect of temperature during this growth stage was on rate of developmental events, i.e. senescence.

DEVELOPMENT

The phenology of the wheat plant is

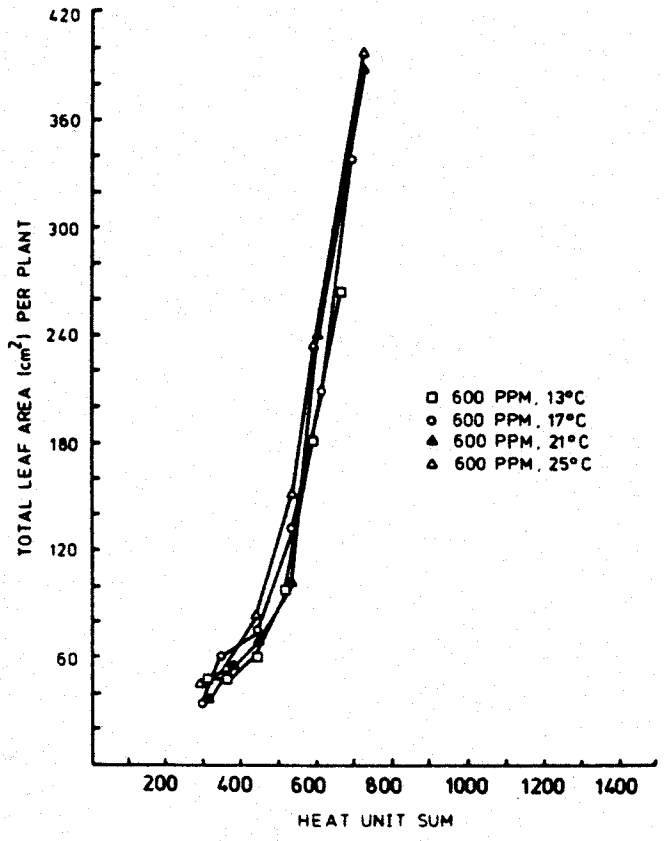

Figure 5. Total leaf area per plant vs. heat units summed above 0°C..

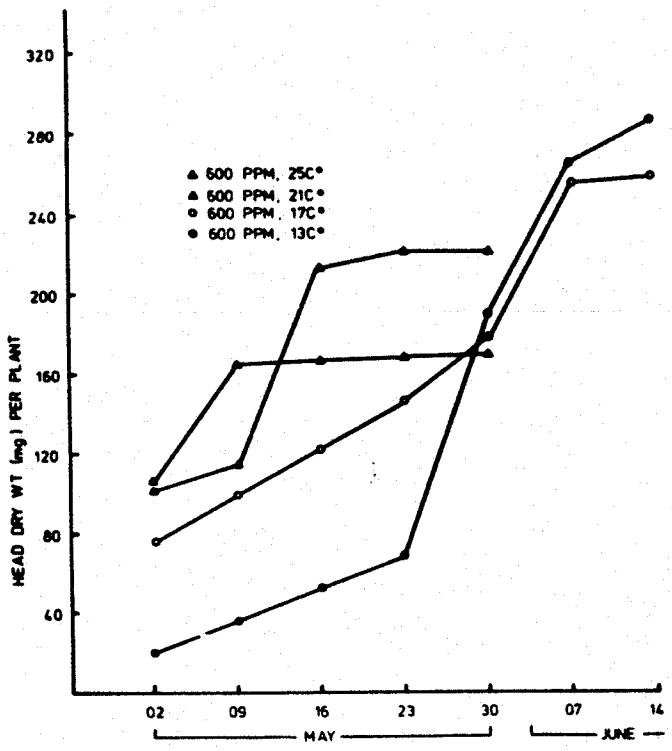

Figure 6. Time courses of head dry weight accumulation at four temperatures.

simulated by estimating the effect of environmental factors on plant developmental rates. As is the case with growth, development records are obtained in SPAR experiments where temperature is controlled and varied systematically in order to characterize the system over the ecological range of interest.

An example of SPAR data describing developmental rates is presented in Figure 7. They are from the 1976 experiment in a 320 µl l^{-1} CO_2 atmosphere. The temperature treatments are presented in Table 1. For use in the simulation model, the stages recorded in Figure 7 and the temperature data in Table 1 are summarized to express

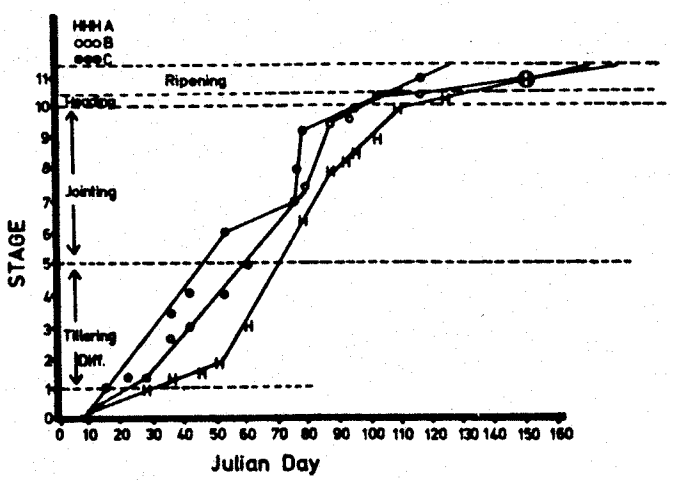

Figure 7. Developmental stage vs. day-of-year (Julian) date for wheat crops maintained in three different temperature regimes.

stage-to-stage developmental transition either as functions of heat unit accumulation from one stage to the next, or as functions of running average temperatures for the periods between stages. Some developmental events may be delayed by physiological stress. Therefore, the rate equations used in the model contain stress terms developed from other SPAR experiments in which various stresses are systematically applied.

Phenological events are only part of the developmental information needed in crop simulation. The initiation, senescence, and abortion of tillers, leaves, and florets must also be recorded in controlled environment experiments.

SUMMARY

The soil-plant-atmosphere-research (SPAR) system was developed as a result of failures in attempts to use models based on field observations of plant responses. Thus, SPAR was designed expressly for the purpose of physiological process level crop simulation modeling. It represented a major advance beyond the classical phytotron in terms of cost and because light and root zone conditions much more closely resembled those in the field. The physiological processes controlled and measured in SPAR experiments in connection with the development of WINTER-WHEAT include photosynthesis, respiration, transpiration, organ growth (including roots) and development. SPAR provides the capability to manipulate stress systematically, permitting the development of models which simulate stress induced senescence and organ abortion.

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